SMALL-SCALE DISTRIBUTION PATTERNS OF A LITTORINID SNAIL ON PILINGS AT JEPARA ON THE NORTH COAST OF JAVA: AN EXPERIMENTAL TEST

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ABSTRACT

A littorinid snail, *Littoraria strigata* (Philippi, 1846), commonly occurring on pilings at the coast of Jepara, North Java, was observed at daytime to aggregate at sea water level irrespective of tidal height, while at night-time the snails dispersed subtidally. It was anticipated that snails occurring on the pilings in a gradient of wave exposure (distance from the shore) showed a gradient in shell morphology. A morphometric analysis revealed that no statistical difference in shell morphology between pilings could be demonstrated but size and weight of the snails was significantly negatively correlated to density. A hypothesis was formulated that aggregation was caused by differences in predation pressure causing higher mortality in subtidal conditions at daytime. The hypothesis was tested by keeping snails on isolated bamboo rods suspended subtidally and intertidally during both day- and night-time conditions. The results showed that snails kept subtidally faced a significant higher mortality during day than at night while no significant difference was found between day and night if snails were kept intertidally.

INTRODUCTION

Most marine hard substratum benthic habitats show a patchy distribution and abundance of organisms in both space and time (Pickett & White 1985; Sebens 1994). In the rocky intertidal patterns of patchiness are pronounced since broad gradients of environmental conditions are superimposed on substratum heterogeneity (Underwood & Denley 1984). Local patchiness or gradients may be caused by gradients of substratum heterogeneity or spatial variation in physical characteristics of the environment, such as temperature and salinity, interacting with biological variables, such as recruitment, competition and predation (see Connell 1972; Dayton 1971; Menge 1991). This array of variables can provide a range of microhabitats within an area of a few square meters.

Spatial patchiness may affect many aspects of the ecology of a variety of intertidal species (Garrity & Levings 1984; Menge 1978a; Menge 1978b; Raffaelli & Hughes 1978; Underwood & Chapman 1989). In contrast to sessile species, mobile species, such as littorinid snails, can potentially select among different microhabitats like pits and crevices where many gastropods shelter during periods of inactivity (Emerson & Faller-Fritsch 1976; Fairweather 1988). Many intertidal gastropods move around to feed irrespective of the time of day but the major exception to this pattern is found among tropical species which tend to move and forage at night (Underwood 1979). However, the ecological significance of this behavioural pattern has not been investigated.

The intertidal gastropod, *Littoraria strigata*, was found abundant on smooth concrete pilings at Teluk Awur (Jepara), supporting a 125 m long pier lending itself to replicated experiments. At daytime, the snails formed dense bands at the air-water interface irrespective of tidal level but dispersed subtidally at nighttime. The aim of the present study is to examine effects of small-scale patterns of distribution on morphometry and test the hypothesis that night-time feeding is an adaptive response to mortality *viz*., differential predation pressure.

MATERIAL & METHODS

Sampling

According to Reid (1986), *Littoraria strigata* (Philippi, 1846) is commonly occurring in mangroves and sometimes found abundant on sheltered rocks and wooden pilings with the main distribution area along the shores of the Malayan Peninsula, Sumatra, Java, Borneo and the Philippines. Specimens of *L. strigata* were sampled from pilings supporting the pier off University Diponegoro Marine Laboratory at Teluk Awur, on the north coast of Java, Indonesia. At Teluk Awur on the coast off Jepara, the snails were found abundant on the pilings but not in the mangrove which was immature and sparse. The pilings had no macroalgal cover and only a few species of sessile animals at very low abundance were found. These were oysters and limpets. Of other mobile fauna one species of crab *(Paragrapsus* sp.) could be observed. During the study the tidal amplitude was about 1 meter.

Height and width of the shells were measured using a stainless steel calliper accurate to 0.01 mm. Whole animals were weighed to the nearest 0.01 gram after drying on filter paper.

To test effects of distribution on morphometry, all snails occurring on 6 separate pilings were sampled (St. 1 - St. 6). The 6 sampled pilings were distributed evenly along the entire 125 m long pier facing south, with Station 1 closest to the shore.

Experimental test

To test the survival effect of submergence, snails were sampled from pilings between the 6 selected stations, pooled and kept in a plastic bucket before use shortly after. A total of 30 snails collected at random from the bucket were distributed on each of the 6 bamboo rods each at a length of 1.5 m. The rods were attached to a 6 mm nylon rope fixed at both ends at the center of the intersections of the bamboo to prevent snails from entering the rope. The rods were suspended from the pier and weighted down in the water by bricks tied to the ropes. Three rods were completely submerged (subtidal) and 3 rods were submerged half (intertidal). After 12 hours the rods were retrieved and the survivors (the snails present on the rods) were counted. No snails were observed to enter the ropes. The experiments were conducted at daytime (0600 h to 1800 h) and at night-time (1800 h to 0600 h) and subsequently repeated. The two experiments were statistically treated as one with 6 replicates at night and day respectively.

Data analysis

The data on morphometry were tested for differences among pilings using a one-way ANOVA. To test for homogeneity of variances the F_{max} test was used. Student-Newman-Keuls test was used to test for differences among means. Only the morphometric variable "weight" was found to be non significant in the F_{max} test and was therefore log(x+1) transformed to obtain a significant normal distribution of the data in order to fulfil the assumption for applying ANOVA. Survival data from the 6 experiments were calculated as percentages, arcsine transformed and tested using a two-factor ANOVA with tidal level and time of day as the main factors. Normality was tested using the F_{max} test. Student-Newman-Keuls test was used to test for differences among means.

In both analysis the computer program SuperAnova (Abacus Concepts Inc. 1991) for the Apple Macintosh was applied (see Walker & Matinez 1993).

RESULTS

Morphometrical analysis

The length-width and length-weight relationships, calculated from all the sampled snails, are shown in Fig. 1. Within the sampled interval, length and width showed a linear relationship with a significant fit (r^2 = 0.892, p<0.001). The length-weight relationship was found to significantly fit a power function (r^2=0.856, p<0.001). To test that snails occurring on the pilings in a gradient of wave exposure (distance from the shore) showed a gradient in shell morphology, a one-factor ANOVA was used on the morphometric data of length, width, and weight. A significant effect of station was found but differences among pilings were not consistent and therefore indicating no correlation with distance from the shore (Fig. 2).

Disregarding Station 2 from the analysis, which had the fewest number of snails (N= 27), a significant negative correlation was found between density and the mean values of the two morphometric variables, length and width (r^2 = 0.80 and 0.79, p<0.05): the higher the number of snails which occurred on a piling, the lower was the mean length and width. Weight was also negatively correlated to density (r^2 = 0.74) but not significantly as the significance level for the linear regression was p = 0.06.

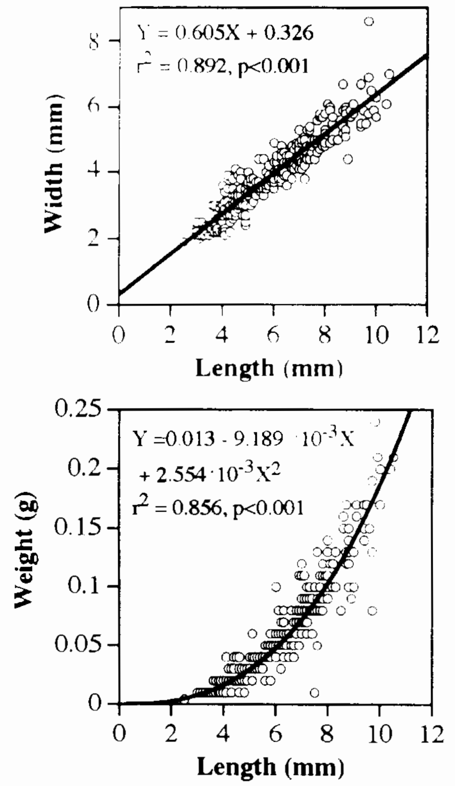

Figure 1. Length width and length weight relationships for the littorinid snail *Littoriaria stigata* (Philippi) occurring on concrete pilings supporting the pier at Teluk Awur (Jepara) on the north coast of Java, Indonesia.

The experimental test of effects of aggregation

A hypothesis was formulated that aggregation was caused by differences in predation pressure causing higher mortality in subtidal conditions at daytime. The hypothesis was tested by keeping snails on isolated bamboo rods suspended subtidally and intertidally during both day- and night-time conditions. A significant effect of time (day/night) was found but no effect of tidal level (half or full submergence) (Tab. 1). Accordingly, snails kept subtidally faced a significant higher mortality during day than night while there was no significant difference between day and night if snails were kept intertidally (Fig. 3). A significant interaction between time and tidal level was found (Tab. 1). The interaction was caused by the synergism observed subtidally between day and night situations (Fig. 3) and accordingly does not interfere with our conclusions. Our experiment thus support the hypothesis that aggregation on the pilings at the air water interface during daytime was caused by differences in predation pressure between day and night.

DISCUSSION

Littorinid snails are commonly found at the highest levels on the sea-shores attributed to physiological resistance to high temperatures, desiccation and the ability to use oxygen from the air (Underwood 1979). Within a local area of occurrence many littorinids show additional small-scale patchiness in distribution, abundance and size-structure, and the existence of morphological gradients have been demonstrated (Chapman 1994; Vermeij 1973). The general patterns seem to be a vertical gradient in size with larger animals found higher on the shore and an inverse relationship between size and density (see Underwood 1979). These patterns may show a large degree of variability within populations and mean size is not simply correlated with wave exposure or periods of desiccation (Chapman 1994). In our study we were not able to show any difference in the morphometric variables length, width and weight along a horizontal gradient of wave exposure and thus agree with Chapman (1994). We did, however, find a significant inverse relationship between density and size. This relationship has been attributed to differential movements of large and small snails towards different heights on the shore and suggest density dependent growth where food is limited at high densities (Gendron 1977; McQuaid 1981). The populations occurring on the pilings at Teluk Awur were all found at the same tidal height and on the same substratum (smooth concrete with little epifauna) indicating that food limitation may be the responsible factor. However, this explanation is difficult to demonstrate experimentally since the available food is not easy to quantify.

Fish predation is an important structuring agent in tropical intertidal communities (Garrity & Levings 1983; Menge *et al.* 1986). Many gastropods are found in so-called "refuge-habitats" both during daytime at low tides and all high tides. They forage actively away from these refuges only for short periods, when physical stress is reduced and

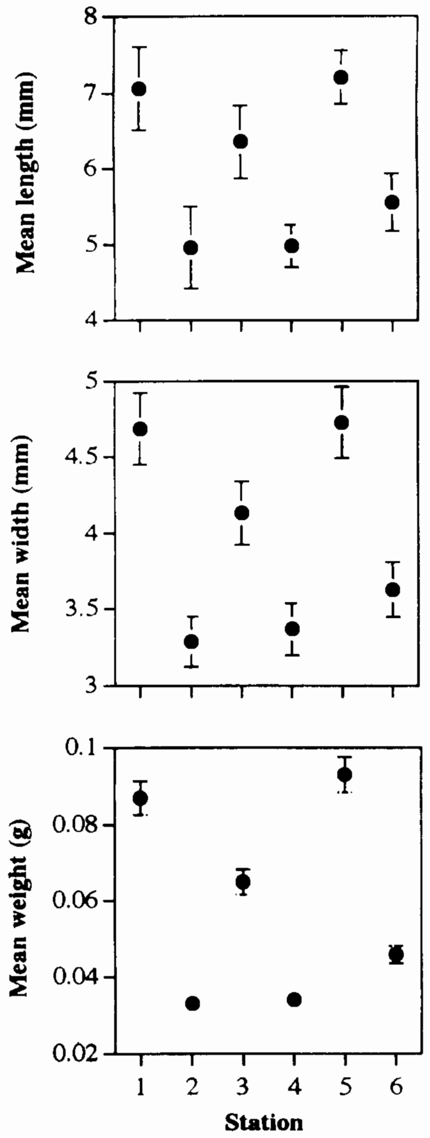

Figure 2. Mean length, mean width and mean weight of the littorinid snail *Littoraria strigata* (Philippi) occurring on 6 concrete pilings evenly distributed along the entire pier at Teluk Awur. Station 1 is closest and station 6 farthest from the shore. Error bars are the 95% C.I.

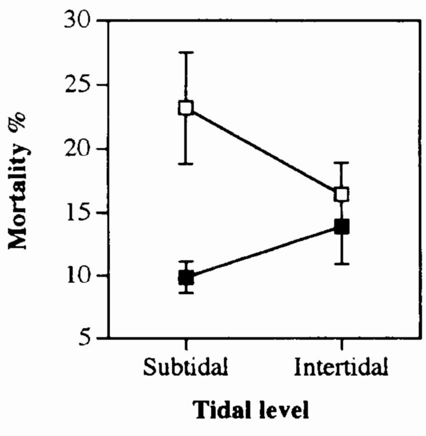

Figure 3. Interaction graph showing the results of a two-factor ANOVA with time (day/night) and tidal level (intertidal/subtidal) as the main factors. Empty symbols = day; filled symbols = night. Error bars are the 95% C.I.

Table 1. Two-factor ANOVA of the experimental data with time and tidal level as the main factors.

Source of variance	df	SS	MS	F-value	P-value
Time	1	374.898	374.989	26.859	0.0001*
Tidal level	1	10.794	10.794	0.773	0.3897
Time x tidal level	1	176.231	176.231	12.623	0.0020*
Residual	20	279.230	13.962		
Student-Newman-Keuls Test					
		Diff.	Crit. diff.	Significance	
Night vs. day		7.906	3.182	*	
Intertidally vs. subtidally		1.341	3.182	n.s.	

exposure to predacious fishes is limited (Garrity 1984). Homing behaviour in limpets, where individual animals return to a particular spot or scar, has been demonstrated as an adaptation to avoid predation since scars provide protection (Garrity & Levings 1983). Limpets forage from and return to scars when the substratum is moistened or wetted by the tides. Similar homing behaviour has not been demonstrated in littorinid snails although these may be found aggregating in pits and scars at low tides (*e.g.*, Chapman 1994).

According to Underwood (1979), many intertidal gastropods move around to feed irrespective of the time of day but the major exception to this pattern is found among tropical species which tend to move and forage at night. The cited studies (Hughes 1971; Kohn & Leviten 1976; Warburton 1973) deals primarily with predatory snails, not herbivorous snails like *L. strigata* in this study. Nevertheless, the ecological significance of this behavioural pattern has not been investigated.

Our observations clearly indicate that snails dispersed during night-time irrespective of tidal level, which was in the range of 1 meter, since the snails followed the tidal movements and were always found at the air water interface at daytime. When snails were aggregating at daytime they were observed to be inactive and non-feeding. Since many tropical predatory fishes are inactive during night and we considered these to be the major predators on *L. strigata,* we conducted an experiment to demonstrate differential mortality. Our results showed a significant higher mortality in snails kept subtidally at daytime compared to night-time while no difference was found between day and night in the subtidal (Fig. 3 & Tab. 1). No significant difference was found between intertidally kept snails irrespective of day or night-time conditions. These results indicate that the observed aggregation behaviour may be adaptive as a response to differential mortality imposed by a higher risk for predation at daytime excursions subtidally. However, since the experimental snails were placed on bamboo rods, which is a rather smooth and slippery substratum, the possibility exist that snails are more likely to fall off when submerged. It was our impression that this was not the case since the snails quickly attached themselves firmly, even on glass.

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